

Factors controlling the decline of net primary production with stand age for balsam fir in Newfoundland assessed using an ecosystem simulation model

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Abstract

Net primary production (NPP) and growth efficiency (wood growth per leaf area) decline with stand age for forest ecosystems. Three hypotheses have been suggested: high respiration to photosynthesis ratios, hydraulic limitations on water transport in trees, and nutrient limitations of photosynthesis. Recent work indicates that hydraulic or nutrient limitations probably are the mechanism underlying the decline of growth efficiency in Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*), both of which are native to western North America. However, balsam fir (*Abies balsamea*) grows in the cool-humid boreal forest and has very high stem respiration rates, suggesting that the mechanism may be different. We predicted measured aboveground NPP of 24 out of 25 balsam fir stands reasonably well. These stands were selected for having large differences in leaf area index and wood mass. Simulations indicate that increased wood respiration is the major factor causing the decline of NPP and growth efficiency with stand age; a secondary factor for mature stands is nitrogen limitation. For simulations in which balsam fir was fertilized, final growth efficiency was less than that of unfertilized forest stands because of increased stem respiration. From values in the literature, we calculated the potential difference conductance to water flow in the xylem from the soil to the leaves for a mean tree in each stand. Twigs had the smallest conductance; however, because the twigs conductances are added in parallel, the bole was the smallest conductance in the series: bole, branch and twigs. The overall drop of water potential with very high transpiration flux densities was generally less than 2.5 MPa. Therefore, we conclude that, for balsam fir, the decline in NPP and growth efficiency with stand age may be caused by the high respiration to photosynthesis ratios. This conclusion differs from recent work, so there is not a single unifying mechanism of age-related decline for all forest ecosystems. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Decline of net primary production (NPP) with stand age has been typically attributed to an

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imbalance of photosynthesis and autotrophic respiration, because stand leaf area index (LAI) reaches a maximum early in stand development whereas the increase in living stems increases the respiratory load. The observation leading to this hypothesis is the decline in growth efficiency, defined as the increment in stem biomass per unit leaf area, with stand age. Gower et al. (1996), Ryan et al. (1997), and Ryan and Yoder (1997) examined the evidence for this and other hypotheses, particularly hydraulic or nutrient limitations.

Autotrophic respiration can be divided into two components (Sprugel et al., 1995). The first is growth respiration, which supplies the energy necessary to convert carbohydrates produced from photosynthesis into new compounds. The second is maintenance respiration, which supplies the energy necessary to continue cellular processes. It is maintenance respiration of the stems which increases the total respiration load. Measurements of stem maintenance respiration have been made for a wide variety of woody plants in different climates and, generally, the rates are low (Ryan et al., 1994a,b, 1995, 1996a; Edwards and Hanson, 1996; Lavigne and Ryan, 1997). Gower et al. (1996) and Ryan et al. (1997) conclude that stem respiration constitutes only a small part of the carbon budget of forests and, thus, is believed unlikely to cause the decline in NPP and growth efficiency.

Stem maintenance respiration rates of balsam fir (*Abies balsamea* (L.) Mill.) are very high in comparison with most other conifers (Lavigne, 1987, 1988; Lavigne et al., 1996a). Similarly, Pacific silver fir (*Abies amabilis*) also has very high stem maintenance respiration rates (Sprugel, 1990). In contrast to the other conifers studied, especially the western lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseudotsuga menziesii*), balsam fir has a very short lifetime and grows in very humid areas, such as in the eastern boreal forest of North America.

We have made extensive measurements of balsam fir structure, growth and respiration in Nfld., Canada (Lavigne et al., 1996a,b); however, these data are insufficient to determine the cause of the decline in NPP and growth efficiency with stand age. We therefore use the ecosystem process simu-

lation model, BGC++, which was derived from BIOME-BGC (Running and Hunt, 1993; Hunt et al., 1996), to ascertain whether the decline in growth efficiency may be due to an increase in maintenance respiration or limitations of either hydraulic transport or nutrients.

2. Materials and methods

2.1. Model description

The model, BGC++, simulates the carbon, water and nitrogen cycles of ecosystems, using two time steps, daily and seasonally (Fig. 1). The use of these two time steps and much of the overall logic of BGC++ derive from BIOME-BGC (Hunt et al., 1996) and FOREST-BGC

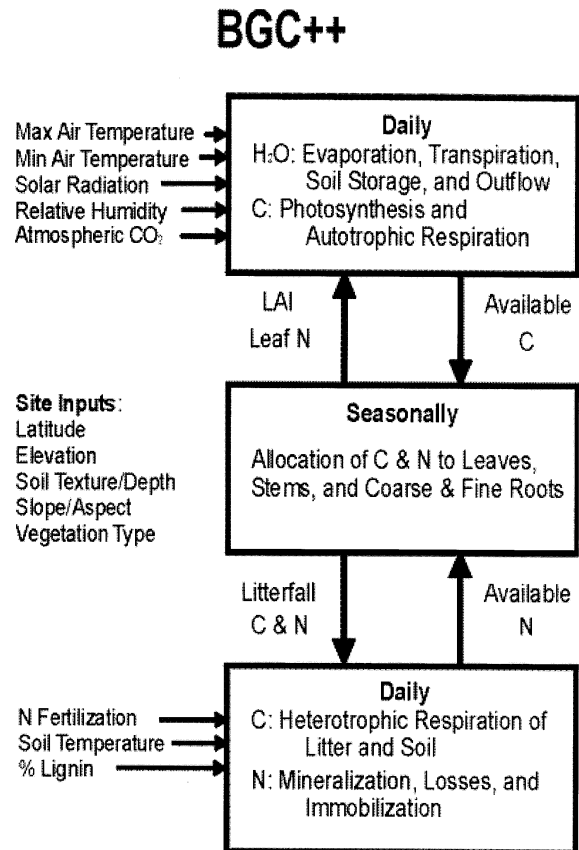


Fig. 1. Flow diagram of BGC++.

Table 1
Values of major parameters of BGC++ for balsam fir

Parameter	Symbol	Value
Specific leaf area	SLA	16.1 m ² kg ⁻¹ C
Optimum temperature	–	20°C
Maximum leaf conductance	g_s	4.0 mm s ⁻¹
Stressed leaf water potential	ψ_{stress}	–1.5 MPa
Leaf respiration rate at 0°C	r_{lf}	0.0012 kg C kg ⁻¹ C day ⁻¹
Stem respiration rate at 0°C	r_{st}	0.0003 kg C kg ⁻¹ C day ⁻¹
Coarse root respiration rate at 0°C	r_{cr}	0.0003 kg C kg ⁻¹ C day ⁻¹
Fine root respiration rate at 0°C	r_{fr}	0.0012 kg C kg ⁻¹ C day ⁻¹
Temperature response for respiration	Q_{10}	2.0
Leaf turnover rate	ω_{lf}	0.20 year ⁻¹
Stem turnover rate	ω_{st}	0.02 year ⁻¹
Coarse root turnover rate	ω_{cr}	0.15 year ⁻¹
Fine root turnover rate	ω_{fr}	0.85 year ⁻¹
Leaf N re-translocation	τ	0.50
Maximum leaf N content	$[\text{N}]_{\text{max}}$	0.035 kg N kg ⁻¹ C
Minimum leaf N content	$[\text{N}]_{\text{min}}$	0.020 kg N kg ⁻¹ C
Leaf lignin content	[lignin]	0.30
Litter N:C ratio	κ_{lit}	0.04 kg N kg ⁻¹ C
Soil N:C ratio	κ_{soil}	0.091 kg N kg ⁻¹ C
Soil organic matter turnover	r_{soil}	0.00025 kg C kg ⁻¹ C day ⁻¹
Maximum leaf/(leaf + fine root)	Λ_{max}	0.67
Allocation stem/(stem + coarse roots)	–	0.85

(Running and Coughlan, 1988; Running and Gower, 1991). The primary difference is that we selected parameters to simulate more closely the physiology of balsam fir (Table 1) instead of the default parameters for evergreen coniferous forests, and we modified the algorithm for allocation considerably (Appendix A).

The daily time step simulates the hydrologic budget, including estimation of soil water content and stomatal conductance, which are strongly determined by LAI with the logic fully described in Hunt et al. (1996). The important driving variables are minimum and maximum air temperatures, relative humidity, solar radiation, and precipitation. Predawn leaf water potential

(ψ_{predawn} , MPa) is calculated from soil water content (W_{soil} , m³ ha⁻¹). Leaf water potential is a function of soil water potential, hydraulic conductivity, and transpiration rate; thus we use ψ_{predawn} to determine water stress, defined as $\psi_{\text{predawn}} < \psi_{\text{stress}}$.

Also estimated in the daily time step procedure are the rates of photosynthesis, autotrophic respiration (sum of growth and maintenance), heterotrophic respiration, and nitrogen transformations (Fig. 1). Photosynthesis is strongly dependent on LAI, which varies considerably for different stands of balsam fir. Photosynthesis and maintenance respiration can be compared in order to determine whether stem respiration is causing the decline in NPP with stand age. Heterotrophic respiration and maintenance respiration of roots are determined by soil temperature, which is estimated from the driving variables listed above (Zheng et al., 1993). The primary daily outputs, which are used by the seasonal time step, are the amounts of carbon and nitrogen available to the vegetation (Fig. 1).

The seasonal (or annual) time step uses the available nitrogen (net N mineralized and N inputs from fertilization minus any losses from the ecosystem) and the available carbon (NPP) to allocate carbon and nitrogen to the state variables for leaves, stems, coarse roots and fine roots (Fig. 1). Furthermore, carbon and nitrogen are transferred from vegetation to the litter (turnover), and from litter to soil organic matter. The algorithm for allocation is based on a ratio of leaf C to the sum of leaf C and fine root C (denoted by Λ). The result of the seasonal time step is the LAI for the next daily time step and the amount of leaf N, which determines the rate of photosynthesis. The ratio of leaf N to leaf C (i.e. the leaf nitrogen concentration, $[\text{N}]_{\text{lf}}$) can be used to determine if the stands are nitrogen limited. The logic of carbon and nitrogen allocation is presented in Appendix A.

2.2. Stand measurements and site description

Twenty-five stands of balsam fir were sampled in western Newfoundland, about 30 km from Corner Brook (48° 55' N, 58° 10' W) to represent

a wide range of densities, diameter classes, stem biomass, and LAI (Lavigne et al., 1996b). The average elevation was 400 m and most of the stands had little slope or aspect. The soils were generally silt loams with an average soil depth of about 1.3 m with about 25% coarse fragments.

Trees were selected by using a prism at ten points for most stands; species and diameters were recorded for each selected tree. Height, height to the base of the live crown, sapwood width, and bark thickness were measured for every fifth tree. Sapwood width and bark thickness were determined in the field from an increment core taken at 1.3 m height, except for four very young stands (trees were 1–3 m tall) for which the measurements were taken at 0.1 m height. Sapwood was

distinguished from heart wood by the translucence caused by water in the conducting tracheids.

Leaves (divided into the top, middle and bottom thirds of the canopy), stems and branches of selected trees were sampled for oven-dry mass, and converted to kg C by assuming biomass was 50% carbon (Table 2). Specific leaf area (SLA $\text{m}^2 \text{kg}^{-1}$ C) was determined from projected needle area using a LI-3100 Leaf Area Meter (LI-COR, Inc., Lincoln, NE, USA) and oven-dry mass of the needles. All-sided leaf area index (LAI, $\text{m}^2 \text{m}^{-2}$) was calculated from SLA and leaf mass (Table 2).

We extended the sapwood width measurements to the entire stand using a regression equation between sapwood area and stem diameter (Lavigne et al., 1996b). The relationship between sap-

Table 2
Structure and growth data for 25 stands of balsam fir in northwestern Newfoundland

ID	Density ($\# \text{ ha}^{-1}$)		LAI ^a ($\text{m}^2 \text{m}^{-2}$)	Diameter (mm)	Height (m)	Stem mass ^b (Mg C ha^{-1})	NPP ^c (Mg C ha^{-1})
	Balsam fir	Total					
3061	3208	3208	4.1	93	6.1	19.5	3.2
3062	82 861	82 999	9.7	37	4.0	70.5	7.0
5022	3574	3585	4.4	125	8.7	48.6	2.1
1031	3499	3985	5.9	125	12.9	69.7	3.1
1039	5094	5110	5.3	98	7.5	32.7	4.4
2004	1937	2265	4.8	152	12.1	61.6	3.2
4010	13 909	14 567	8.3	66	7.2	56.1	5.3
1054	2685	3112	3.9	90	6.5	19.6	3.0
4033	1060	1108	3.5	214	14.0	63.9	1.6
2053	2662	3204	6.2	141	12.9	71.2	4.1
3028	2589	2606	4.8	151	12.2	71.1	1.3
6009	4882	4882	6.2	112	8.4	55.4	3.0
6006	2043	2408	3.8	157	11.6	57.1	2.5
1072	1120	1242	3.5	193	15.5	61.8	2.3
6019	1243	1416	3.3	188	15.6	65.1	2.0
2008	12 006	12 227	6.9	69	7.2	51.4	2.1
1039	4986	5887	5.9	104	10.4	60.7	4.3
6029	2510	2510	3.3	82	5.2	14.1	2.5
2048	1875	1969	4.0	160	12.0	56.2	1.1
3023	1504	1615	3.7	175	13.1	64.4	1.2
5035	1601	1630	4.1	172	12.4	53.7	1.8
4001	90 833	93 000	7.8	27	1.9	22.2	4.8
1040	139 000	144 000	13.1	25	1.9	37.0	5.8
5025	146 500	149 500	10.2	22	1.9	33.0	5.6
1055	136 000	144 000	9.2	22	1.9	30.2	5.7

^a Ratio of all-sided (total) leaf area to projected leaf area is 2.3.

^b Assumes dry matter is 50% carbon.

^c Aboveground net primary production.

wood area and leaf area (Lavigne et al., 1996b) was used to determine the sapwood area for top, middle and bottom thirds of the canopy. Sapwood area was multiplied by height to calculate sapwood volume and sapwood mass. We regressed sapwood mass versus total stem mass for calculations of stem respiration. Rates of stem respiration were measured on four of these stands (Lavigne et al., 1996a) and these rates were used to parameterize BGC++.

For the stems and branches, the width of the most recent ring was used to determine the diameter growth. The mass of the current-year needles was used to determine leaf growth. These growth measurements were again scaled to the stand using allometric equations based on tree diameter to calculate aboveground net primary production (Table 2).

2.3. Model simulations

We conducted two sets of simulations; the first set was to test simulated NPP with estimated NPP for the 25 stands in western Newfoundland. We used the stem masses and LAI from Table 2 to initialize these state variables. Following the logic of Hunt et al. (1996), other state variables were assigned reasonable values based on stem mass and LAI. We used the boreal forest average soil carbon mass from Hunt et al. (1996), and average nitrogen concentrations measured for five stands (Lavigne et al. 1996a). Given that we estimated net primary production for 1992, we used the 1992 daily meteorological data from Deer Lake because Corner Brook has more of a maritime climate. Hence, the meteorological data were closer to the actual precipitation and air temperatures experienced by the 25 stands.

The second set of simulations was used to determine the variables and parameters associated with stand decline with age. We started with a young regenerating stand of balsam fir and followed NPP and other variables over 100 years. Because we did not have a long time series of meteorological data for western Newfoundland, we used the 1992 Deer Lake data repeatedly. To determine if the decline of NPP and growth efficiency with stand age was caused by nitrogen

limitation, we simulated a regenerating stand fertilized with 20 kg N ha⁻¹ annually. To determine if soil water deficits directly caused the decline in NPP, we simulated a regenerating stand irrigated with 5 mm of rain or snow daily, which kept the soil at maximum volumetric water content.

2.4. Calculation of water potential difference in xylem

If large, the difference in water potential from the soil (ψ_{soil} , MPa) and the leaf (ψ_{leaf} , MPa) through the xylem may lead to cavitation and embolism, thus rendering the tracheid useless for the conduction of water (Tyree and Sperry, 1989; Tyree and Ewers, 1991). Given the simulated transpiration rates from the BGC++ model using the Penman–Monteith equation, and the total potential difference conductance (L_{total} , m³ s⁻¹ MPa⁻¹; Hunt et al., 1991b), we calculated the difference between ψ_{soil} and ψ_{leaf} to determine if the difference was larger than that which would cause cavitation. Sperry and Tyree (1990) showed that for balsam fir, the difference in water potential that would cause 50% loss in hydraulic conductivity is 2.5 MPa (their Fig. 4a). Furthermore they determined that the potential-gradient conductivity (cf. Hunt et al., 1991b), which they termed the specific conductivity, was 1.2 kg s⁻¹ MPa⁻¹ m⁻¹ based on sapwood area. This potential-gradient conductivity converts to 1.2×10^{-3} m² s⁻¹ MPa⁻¹ and is multiplied by sapwood area (m²) and divided by segment length (m) to obtain the potential difference conductance of that segment.

We determined the dimensions of a mean tree for each stand. For the bole, we took the height to be the sum of the height to the base of the live crown and one-half the height of the crown. Because water transport works against gravity, we added 0.01 MPa per meter height of the bole to the water potential difference. For branches, we took the length to be one-half of the height of the crown. For twigs, we assumed a length of 5 cm (one-half an average length of 10 cm). The number of branches was estimated from the stand branch mass divided by 0.5 kg branch⁻¹. Sapwood area of each branch was assumed to be 0.1

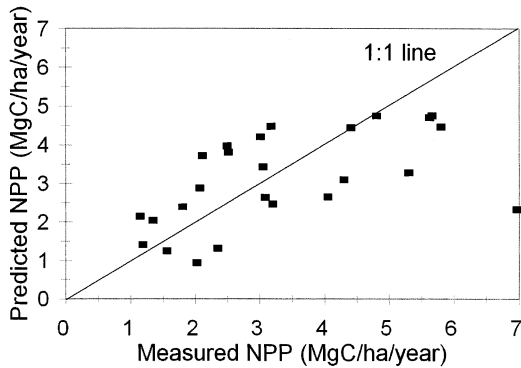


Fig. 2. Predicted and measured aboveground net primary production for 25 stands of balsam fir in western Newfoundland. The line is $y = x$, and not a fit to the data. The goodness of fit to the $y = x$ line (similar to R^2) is 0.74.

of the bole sapwood area. Data from Ewers and Zimmermann (1984; fig. 3) suggest this assumption is reasonable. The number of twigs was estimated from the mean leaf area per tree divided by $30 \text{ cm}^2 \text{ twig}^{-1}$. The sapwood area of the twigs was assumed to be 0.003 cm^2 . Total branch and twig potential difference conductances were obtained by adding the separate branch and twig conductances in parallel; L_{total} was calculated by adding the bole, total branch and total twig conductances in series.

3. Results and discussion

3.1. Comparisons of simulations with stand data

The predicted aboveground NPP matched well the measured NPP of balsam fir stands, except for one stand (ID number 3062) with high stem mass, LAI, and tree density (Fig. 2). The 1:1 line in Fig. 2 was not determined from a linear regression. The goodness of fit to the 1:1 line (where $\hat{y} = x$) was 0.74.

The prediction error for stand 3062 (about 65%) cannot be explained by normally occurring errors of measurement or simulation. The number of possible explanations is infinite, so in this situation, logic suggests the simpler explanations be preferred. This was one of the stands used to measure respiration rates (Lavigne et al., 1996a);

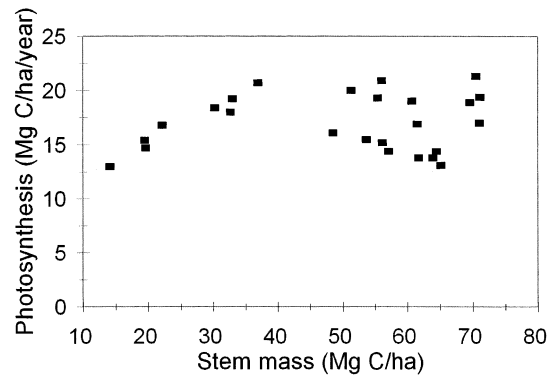


Fig. 3. Simulated annual photosynthesis for the measured balsam fir stands.

therefore, the stand did not reduce its respiration load with increasing NPP. A simple explanation is that the allometric equations we used were not appropriate for this stand because of its extremely high stem density (Table 2).

For the mature stands, the annual sum of daily photosynthesis simulated over the growing season varied from about 13 to $22 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ (Fig. 3). Simulated respiration for the year included both growth and maintenance of leaves and stems, and totalled up to 63% of annual photosynthesis (Fig. 4). Even for young stands, aboveground respiration was a significant fraction (33%) of annual photosynthesis. With fine and coarse roots included, autotrophic respiration accounted from 52 to 85% of annual photosynthesis.

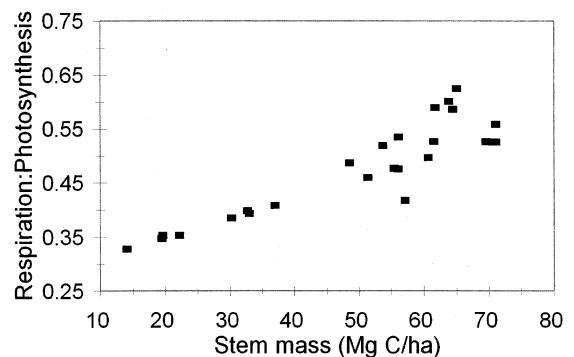


Fig. 4. Simulated ratio of annual aboveground respiration to annual photosynthesis for the measured balsam fir stands. Respiration includes both growth and maintenance for leaves and stems.

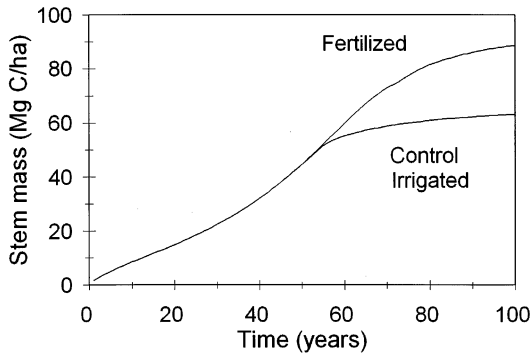


Fig. 5. Simulated change in stem mass over time for control, fertilized, and irrigated balsam fir stands.

These values are much higher than the range, 33–64%, reported by Ryan et al. (1996a) for pines. The high maintenance respiration rates of balsam fir sapwood (Lavigne, 1987, 1988; Lavigne et al., 1996a) are a significant fraction of the annual carbon budgets. Because the measured stands were chosen specifically to represent a wide range of densities, LAI and stem biomass, the increase in the ratio of respiration to photosynthesis with stem mass (Fig. 4) can not be used to indicate which hypothesized mechanism is responsible for the decrease in NPP and growth efficiency with stand age.

3.2. Long-term simulations

Stem growth of the control and irrigated stands was equal over time, showing no effect of added water to balsam fir in western Newfoundland (Fig. 5). In contrast, additional fertilizer substantially increased wood production, but only after 60 years (Fig. 5). The increase in stem mass was matched by an increase in leaf area index up to 52 years for the control and irrigated stands, then LAI declined and maintained a steady value (Fig. 6). The small reduction in LAI was caused by the strong water limitation (Eq. (A.8)). The fertilized stand continued the increase in LAI to 73 years, then declined and maintained a steady value (Fig. 6). Net primary production closely followed the dynamics of LAI for control, fertilized and irrigated stands (Fig. 7). In year 100, fertilization of balsam fir more than doubled the final value of

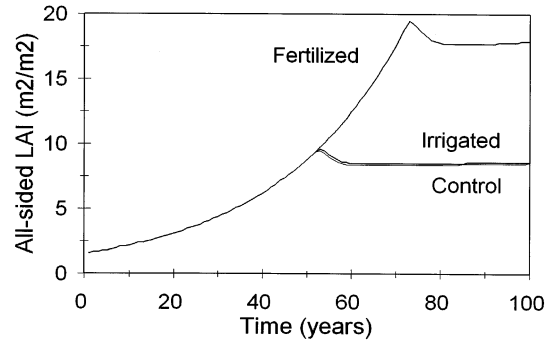


Fig. 6. Simulated change in leaf area index (all-sided) over time for control, fertilized, and irrigated balsam fir stands.

LAI, and increased the final value of NPP by 80%, but did not change the dynamics of early stand growth (Figs. 5–7). For all three simulations, predawn leaf water potentials never reached the level defined as stressful, ψ_{stress} (Table 1), indicating that hydraulic limitation of NPP for balsam fir is highly unlikely.

Growth efficiency declines rapidly after a peak in year 3; the decline is smaller as the stand ages, and then declines rapidly again in year 52 for the control and irrigated stands (Fig. 8). The fertilized stand has different dynamics after year 52, and interestingly, the final growth efficiency is lower for the fertilized stand because of the extra stem mass. For the first 40 years, $[N]_{\text{fr}}$ is at the maximum possible value for control, irrigated and fertilized stands, and $[N]_{\text{fr}}$ reaches the minimum value at the end of the 100-year simulation (Fig.

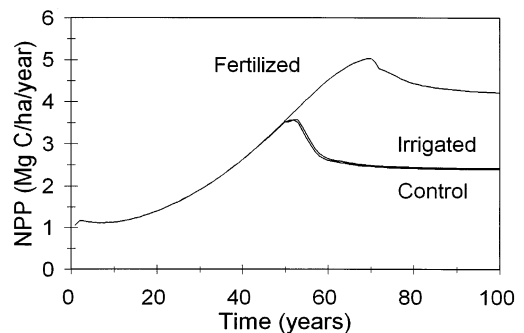


Fig. 7. Simulated change in aboveground net primary production over time for control, fertilized and irrigated balsam fir stands.

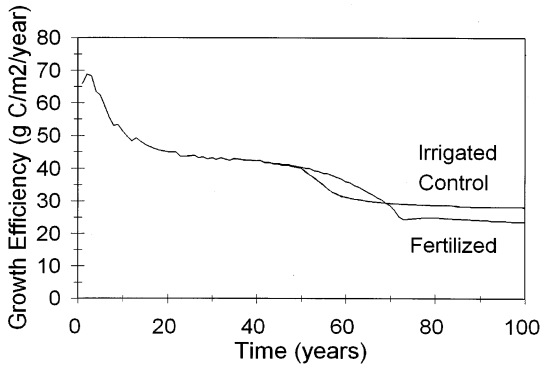


Fig. 8. Simulated change in growth efficiency over time for control, fertilized and irrigated balsam fir stands.

9). Fertilization controls when the leaves become nutrient stressed but not the final values. Thus, nutrient limitation plays a role in decline of growth efficiency of balsam fir after the stands reach maturity. Respiration by sapwood is the major limitation throughout the time period of the simulation controlling the decline in growth efficiency (Fig. 8).

Murty et al. (1996) analyzed the respiration, hydraulic, and nutrient hypotheses for the age decline in growth efficiency using another ecosystem process model, G'DAY. In water limited ecosystems of lodgepole pine, nutrient limitations were one factor in stand decline, and hydraulic limitation may or may not occur depending on model assumptions. The one proposed mechanism

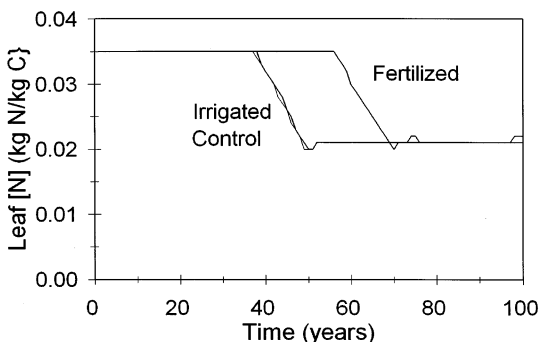


Fig. 9. Simulated change in leaf nitrogen concentration over time for control, fertilized and irrigated balsam fir stands. The maximum leaf concentration, $[N]_{\max}$, was set to be $0.035 \text{ kg N kg}^{-1} \text{ C}$ and the minimum leaf concentration, $[N]_{\min}$, was set to be $0.02 \text{ kg N kg}^{-1} \text{ C}$.

of stand decline not supported by Murty et al. (1996) was increased respiration with increased stem mass.

3.3. Calculation of water potential difference in balsam fir

As shown before (Tyree and Sperry, 1989; Tyree and Ewers, 1991), the potential difference conductance for a single twig was $7.2 \times 10^{-9} \text{ m}^3 \text{ s}^{-1} \text{ MPa}^{-1}$, which is two to three orders of magnitude smaller than the potential difference conductance for the bole of a mean tree for each stand (Table 3). Potential difference conductances for mean branches were smaller than the conductances for the bole, but not ten times smaller because of the smaller length assumed for the branches. Therefore the largest drop in water potential for a particular leaf occurred in the twig, and cavitation when it occurred would occur at this location (Tyree and Ewers, 1991). However, because of parallel paths of water transport in the branches and twigs, the smallest conductance in the series from soil to the air was that of the bole (Table 3).

BGC++ simulates transpiration on a daily time step; intermediate variables were extracted in order to calculate instantaneous transpiration rate at solar noon. Preliminary calculations indicated the simulated transpiration flux densities would cause differences between ψ_{soil} and ψ_{leaf} to be only 0.5 MPa during the growing season. Therefore, we selected daily conditions to be a very sunny and warm day in western Newfoundland. The maximum air temperature was 25°C , intercepted solar radiation was 550 W m^{-2} , the vapor pressure difference was 1.8 kPa, and stomatal conductance was 3 mm s^{-1} . From the Penman–Monteith equation, the transpiration flux density was $5.3 \times 10^{-8} \text{ m}^3 \text{ m}^{-2} \text{ s}^{-1}$, which corresponds to 4.2 mm day^{-1} of transpiration by the stand.

The instantaneous transpiration flux density was converted to a volume flow, and the difference between ψ_{soil} and ψ_{leaf} was calculated (Table 3). Only two of the 25 stands had calculated differences greater than 2.5 MPa, the value for cavitation determined by Sperry and Tyree (1990).

Table 3

Calculations of potential difference conductances for water flow through the bole, branches and twigs of the balsam fir stands

ID	Bole		Branches			Twigs		Total	
	SW ^a	L_t ^b	N ^c	L	L_t	N	L_t	L_{total}	$\Delta\psi$ ^d
3061	41.8	1200	10	250	2600	5847	42 000	800	1.2
3062	3.8	140	1	61	61	530	3800	42	2.0
5022	37.1	640	9	250	2200	5190	37 000	490	1.7
1031	44.9	520	11	230	2500	6283	45 000	420	2.4
1039	42.0	940	10	230	2500	5883	42 000	670	1.4
2004	53.3	650	14	280	4100	7467	55 000	550	2.2
4010	16.9	350	4	130	530	2360	17 000	210	1.9
1054	38.5	960	9	270	2500	5390	39 000	690	1.3
4033	83.1	950	25	280	6900	11 637	84 000	830	2.3
2053	54.1	610	13	290	3800	7570	55 000	520	2.4
3028	45.6	540	11	260	2900	6387	46 000	450	2.3
6009	33.5	570	8	310	2400	4683	34 000	450	1.7
6006	50.3	840	13	140	1800	7037	51 000	570	2.0
1072	72.2	740	19	230	4500	10 113	73 000	630	2.6
6019	66.0	630	18	260	4700	9243	67 000	550	2.8
2008	15.5	290	4	230	930	2167	16 000	210	1.7
1039	31.2	410	8	300	2300	4363	31 000	340	2.1
6029	31.7	1100	7	230	1700	4440	32 000	640	1.1
2048	50.3	640	12	240	2800	7037	51 000	510	2.3
3023	57.9	650	15	300	4400	8103	58 000	560	2.4
5035	68.0	850	17	290	5000	9523	69 000	720	2.2
4001	3.0	380	1	38	38	417	3000	34	2.0
1040	2.4	300	1	30	30	333	2400	27	2.0
5025	1.7	220	1	22	22	243	1800	20	2.0
1055	1.7	230	1	23	23	240	1700	21	1.9

^a Sapwood area (cm²) of the mean tree.^b L , L_t , and L_{total} are the potential difference conductance ($\times 10^{-9} \text{ m}^3 \text{ s}^{-1} \text{ MPa}^{-1}$) for the individual segment (a branch or twig), total for the bole, branches, or twigs, and total through the tree, respectively.^c Number of segments in parallel.^d Difference between ψ_{soil} and ψ_{leaf} (MPa).

On the other hand, there was a positive, significant relationship between the water potential difference and bole diameter ($\Delta\psi = 1.53 + 0.041$ diameter, $R^2 = 0.31$). This indicates there may be a hydraulic limitation for large trees of balsam fir, because these stands also had among the lowest aboveground NPP. However, the conditions we chose for the transpiration flux density were selected to get a large difference between ψ_{soil} and ψ_{leaf} . Furthermore, the capacitance (water storage) was neglected in these calculations. Because of the sizable volume of water stored in the stems (Hunt et al., 1991b), it is unlikely that the differences between ψ_{soil} and ψ_{leaf} would be sufficiently large to cause a significant hydraulic limitation.

3.4. Model testing using regional and stand net primary production data

One of the most important questions for the use of ecosystem simulation models in examining hypotheses of forest processes is, what kind of data are important for model testing? We do not want to discuss various philosophical issues concerning model validation and testing; however, any conclusions drawn from the simulations presented above depend on the credibility of BGC++. Being derived from BIOME-BGC, this model has a long history of development and testing (Running and Hunt, 1993).

Lauenroth and Sala (1992) showed that relationships between precipitation and net primary production of grassland ecosystems were different depending on whether a precipitation gradient or year-to-year variations was used. The slope of NPP versus annual precipitation for a precipitation gradient was 4.6 times that determined from long-term forage production data. Similarly, the FOREST-BGC model was tested using a precipitation gradient across Oregon (Running, 1994; Runyon et al., 1994) and using stem-analysis data (Hunt et al., 1991a). Again the slope of measured NPP versus annual precipitation for the precipitation gradient in Oregon was much higher than the slope obtained from year-to-year variations.

Lauenroth and Sala (1992) conclude from their data that there is a major problem in exchanging space for time, because vegetation type constrains the response of NPP to precipitation. In other words, along the climatic gradient, vegetation is adapted to different mean conditions. Therefore, the ability of a model to adequately represent two or more ecosystem processes constrained by vegetation type is a difficult test. The results presented in Fig. 2 indicate that BGC++ is able to simulate NPP when both stem mass and LAI are independently varied (through stand selection).

On the other hand, NPP is the difference between photosynthesis and respiration. There may be large errors simulating both processes, which are masked by the comparison of measured and predicted NPP (Fig. 2). Hunt et al. (1996) present how BIOME-BGC simulates the discrimination of ^{13}C ; the stable carbon isotope ratio of vegetation is calculated from water use efficiency, the ratio of transpiration and photosynthesis. Therefore, the stable carbon isotope ratio is constrained by two ecosystem processes, which are independently simulated. Of course, transpiration is usually constrained by the amount of precipitation, so constraints cascade through the ecosystem. Another measurement constrained by two or more ecosystem cycles is the net mineralization of nitrogen.

To sum up, the difficulty of testing should be a major criterion for model credibility. The more difficult tests are when the data are strongly constrained by vegetation type at a single location.

Variables used for testing should be at the intersection of two or more ecosystem processes because if the model simulates several processes, then each ecosystem process is constrained by the others.

4. Conclusions

Gower et al. (1996) and Ryan et al. (1997) have examined the available evidence supporting or rejecting the three major hypotheses explaining the decline of growth efficiency with forest stand age. The first two are an imbalance between respiration and photosynthesis and a limitation by nutrients. The third and their favored hypothesis is that a hydraulic limitation imposes water stress. Based on the evidence, they concluded that an imbalance between respiration and photosynthesis was not likely to occur, thereby supporting the two other hypotheses.

The simulations and calculations presented here provide evidence that for balsam fir at least, an imbalance between respiration and photosynthesis is the most likely explanation. Simulations of stand growth over time show a strong decline related to the accumulation of respiring mass. The simulated decline is not stopped with nitrogen or water additions. Calculations show that a hydraulic limitation may occur in older trees, but under conditions not usually found in cool-humid western Newfoundland. Conifers in western North America and similar climates experience drought frequently, and are probably more susceptible to hydraulic limitations. Therefore, the objective of developing a single, unifying mechanism to explain the decline of NPP and growth efficiency with stand age may not be possible.

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Appendix A. Description of the seasonal time step for allocation of carbon and nitrogen to leaves, stems, coarse roots, and fine roots

The state variables of BGC++ are the same as those in BIOME-BGC (Hunt et al., 1996, Fig. 1) and are the carbon contents (kg C ha^{-1}) of leaves (M_{lf}), stems (M_{st}), coarse roots (M_{cr}), fine roots (M_{fr}), litter (M_{lit}), and soil (M_{soil}). Additional state variables are the nitrogen contents (kg N ha^{-1}) of leaves (X_{lf}), stems (X_{st}), coarse roots (X_{cr}), fine roots (X_{fr}), litter (X_{lit}), and soil (X_{soil}). Available carbon for growth (M_{avail}) is the total daily photosynthesis minus the sum of daily maintenance respiration of leaves, stems, coarse roots, and fine roots. Turnover reduces the vegetation carbon contents and adds the carbon to the litter:

$$M_{\text{lit}}(t) = M_{\text{lit}}(t-1) + \omega_{\text{lf}} M_{\text{lf}} + \omega_{\text{st}} M_{\text{st}} + \omega_{\text{cr}} M_{\text{cr}} + \omega_{\text{fr}} M_{\text{fr}} \quad (\text{A.1})$$

where: ω is the turnover rate parameter (Table 1); t is the current seasonal time step; $t-1$ is the previous seasonal time step; and M_{lf} , M_{st} , M_{cr} , and M_{fr} are reduced to maintain mass balance. Nitrogen is added to the litter:

$$X_{\text{lit}}(t) = X_{\text{lit}}(t-1) + (1-\tau)\omega_{\text{lf}} X_{\text{lf}} + \omega_{\text{st}} X_{\text{st}} + \omega_{\text{cr}} X_{\text{cr}} + \omega_{\text{fr}} X_{\text{fr}} \quad (\text{A.2})$$

where: τ is the fraction of nitrogen re-translocated from the senescing leaves; $\tau \omega_{\text{lf}} X_{\text{lf}}$ is added to the available nitrogen for growth (X_{avail}), and X_{lf} , X_{st} , X_{cr} , and X_{fr} are reduced to maintain mass balance. We assume fine roots do not re-translocate nitrogen upon senescence.

Carbon and nitrogen are transferred from litter to soil based on the lignocellulose hypothesis of Melillo et al. (1989). The lignin in litter is resistant to decomposition by soil heterotrophs and is the primary compound transferred to soil organic matter:

$$M_{\text{soil}}(t) = M_{\text{soil}}(t-1) + [\text{lignin}]M_{\text{lit}}(t-1) \quad (\text{A.3})$$

where [lignin] is the lignin concentration of leaves. The litter is assumed to have the ideal nitrogen concentration to become soil organic matter, so:

$$X_{\text{soil}}(t) = X_{\text{soil}}(t-1) + \kappa_{\text{soil}}[\text{lignin}]M_{\text{lit}}(t-1) \quad (\text{A.4})$$

where: κ_{soil} is the nitrogen:carbon ratio of soil organic matter (Parton et al., 1987); and X_{lit} is reduced to maintain mass balance.

M_{soil} is reduced by respiration (turnover) from soil heterotrophs calculated daily; the total nitrogen mineralized is calculated by $\kappa_{\text{soil}} \sum r_{\text{soil}} M_{\text{lit}}$, and subtracted from X_{soil} . Nitrogen immobilization is calculated by comparing the ratio $X_{\text{lit}}:M_{\text{lit}}$ with a critical litter N:C ratio, κ_{lit} (Table 1). If $X_{\text{lit}}:M_{\text{lit}}$ is greater than κ_{lit} , then nitrogen is released, whereas if $X_{\text{lit}}:M_{\text{lit}}$ is less than κ_{lit} , then nitrogen is immobilized (Berg, 1986). Nitrogen losses from the ecosystem are estimated based on Johnson (1992). Available nitrogen (X_{avail}) is the sum of nitrogen mineralization from the soil, nitrogen fertilization or fixation, and nitrogen re-translocated from leaf turnover, minus nitrogen immobilization and nitrogen losses from the ecosystem.

The relative allocation of carbon and nitrogen between leaves and fine roots is based on two values. Theoretically, we expect that if nitrogen and soil water are plentiful, then vegetation would preferentially allocate C and N to leaves, whereas if water or nutrients were not sufficient, then vegetation would allocate more C and N to fine roots. The first is the water stress integral (Myers, 1988), which is the sum of predawn leaf water potential (ψ_{predawn} , MPa) over the time period. We normalized the water stress integral (WSI) from 0 to 1 by comparing it with water potential sums of no stress and constant stress ($\sum \psi_{\text{stress}}$) over the time period. The second is an index of nitrogen availability (N_{index}) defined as the ratio of X_{avail} to the nitrogen required to replace that lost by turnover (with a maximum index equal to 1). We define Λ to be the proportion of carbon allocated to leaves compared with the total carbon available for both leaves and fine roots. Λ is calculated from the water stress integral and nitrogen availability index:

$$\Lambda = \Lambda_{\text{max}}(\text{WSI} + N_{\text{index}}) \quad (\text{A.5})$$

where Λ_{\max} is the maximum value of the leaf/ (leaf + fine root) ratio (Table 1).

From FOREST-BGC (Running and Gower, 1991), the amount of carbon allocated to the leaves (η_{lf} , kg C ha⁻¹) is the minimum value of three limits: a carbon limit, a nitrogen limit and a water limit. The Running and Gower (1991) formulation was not robust and must be tuned for each site. Based on BIOME-BGC simulations of the Swedish Conifer and the Biology of Forest Growth experiments (Ryan et al. 1996b), we concluded a new formulation was required. Therefore, allocation of carbon to the leaves is the minimum of:

$$\eta_{\text{lf}} = \Lambda M_{\text{avail}} \quad (\text{carbon limit}) \quad (\text{A.6})$$

$$\eta_{\text{lf}} = \Lambda X_{\text{avail}} / [\text{N}]_{\text{min}} \quad (\text{nitrogen limit}) \quad (\text{A.7})$$

$$\eta_{\text{lf}} = \Lambda (M_{\text{lf}} + M_{\text{fr}}) (W_{\text{soil}} / W_{\text{max}}) \quad (\text{water limit}) \quad (\text{A.8})$$

where: $[\text{N}]_{\text{min}}$ is the minimum possible leaf nitrogen concentration (Table 1); W_{soil} is the current amount of water stored in the soil (m³ ha⁻¹), and W_{max} is the maximum amount of soil water storage. The use of $(W_{\text{soil}} / W_{\text{max}})$ is from Woodward (1987). If W_{soil} is equal to W_{max} , then $0.85 W_{\text{max}}$ is used in Eq. (A.8) thereby increasing η_{lf} . Relative allocation to the fine roots is $1 - \Lambda$. If the vegetation is carbon limited, then there is no carbon available for stems and coarse roots. If vegetation is water or nitrogen limited, then the carbon remaining after allocation to leaves and fine roots is distributed between stems and coarse roots using a constant fraction (Table 1). After carbon is allocated, then a fraction is lost for growth respiration, which was calculated daily as a constant fraction of photosynthesis.

The allocation of nitrogen to leaves is determined by the leaf nitrogen concentration ($[\text{N}]_{\text{lf}}$, kg N kg⁻¹ C):

$$[\text{N}]_{\text{lf}} = \Lambda X_{\text{avail}} / \eta_{\text{lf}} \quad (\text{A.9})$$

where $[\text{N}]_{\text{lf}}$ is allowed to vary between $[\text{N}]_{\text{min}}$ and a maximum leaf nitrogen concentration ($[\text{N}]_{\text{max}}$). The nitrogen concentration of fine roots is assumed to be $0.5 [\text{N}]_{\text{lf}}$, whatever nitrogen available remains is distributed between stems and coarse roots with a constant fraction (Table 1).

Photosynthetic parameters of the Farquhar et al. (1980) model for the maximum rate of carboxylation (V_{max} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and light reactions (J_{max} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) are determined as a function of $[\text{N}]_{\text{lf}}$. The Farquhar et al. (1980) photosynthetic model was originally implemented in BIOME-BGC by Hunt and Running (1992). We set J_{max} as a function of V_{max} (Wullschlegel, 1993). We used a linear relationship between V_{max} and $[\text{N}]_{\text{lf}}$ from Evans (1989) (Fig. 2) where 6% of the leaf N is used for RuBP carboxylase, in order to get the response of maximum photosynthetic rate similar to that of other conifers (Teskey et al., 1995, Fig. 2). One problem we had was using the overall relationship between photosynthetic rate and $[\text{N}]_{\text{lf}}$ as reviewed by Field (1991) (Fig. 1). The slope of the overall regression equation is much higher than for a single species, which caused model instabilities. Thus, there may be a limit in the value of large-scale datasets for parameterizing ecosystem models.

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